

The University of Chicago

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DOMINANCE-SUBORDINATION
RELATIONSHIP IN THE FISH
PLATYPOECILUS MACULATUS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF ZOÖLOGY
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SOME ASPECTS OF THE DOMINANCE-SUBORDINATION RELATIONSHIP IN THE FISH *PLATYPOECILUS MACULATUS*¹

JAMES CONGER BRADDOCK

Whitman Laboratory, University of Chicago²

THIS paper is not offered as a complete analysis of the social behavior of *Platypoecilus maculatus* but rather as an introduction to the topic. Descriptions of the actual bodily movements of individual fishes approach the "natural-history" type of presentation. This approach is open to criticism, but it does permit the reader more clearly to visualize the characteristic behavior of the fishes; the movements of individuals of this species are stereotyped enough and the experimental procedures are sufficiently precise to permit this type of treatment. The work on this problem to date has been exploratory, and the hypotheses presented are tentative. Further experimental analyses are planned.

Dominance-subordination relationships have been demonstrated for many vertebrate types (Collias, 1944). The pioneer work in this field was done by Schjelderup-Ebbe, who in 1922 described in detail the social order in chickens and referred to various social relationships in other birds in a more general way. Allee and his associates have reported a series of detailed studies on the subject, and Allee (1931, 1938, 1940, 1942, 1943) has worked toward integrating many of the social factors into an orderly plan. The late G. K. Noble and his associates (1936,

1938, 1939a, b, 1940, 1941) did the preliminary work on social orders in fishes, with special attention to the cyclid *Hemichromis bimaculatus* (Noble and Curtis, 1939) and the poecilid *Xiphophorus helleri* (Noble, 1939; Noble and Borne, 1940).

THE EXPERIMENTAL ANIMAL AND ITS TREATMENT

Platypoecilus maculatus was chosen as the experimental animal for this work because of its conveniently small size, relatively high belligerency, and color patterns that are variable enough to make identification of individual fishes certain even when they are in continual and fairly rapid motion. The fishes were obtained in part from local dealers, in part from large-scale breeders.

The various experimental conditions are presented in tabular form in Table 1. The lamps referred to in the table are ordinary goosenecked student lamps. The artificial pond water³ is a preparation which experience has shown to be a favorable medium for the maintenance of various fresh-water animals. All of the aquaria contained gravel but no plants, with the exception of the large greenhouse tank, which had plants at both ends but not in the middle portion.

An effort was made to begin taking observations at the same time each day. Also, the various aquaria were always observed in the same order.

³ Formula for artificial pond water: distilled H₂O plus the following salts: 100 mg/liter, CaCl₂·4H₂O; 50 mg/liter, K₂SO₄; 50 mg/liter, MgSO₄·7H₂O; 50 mg/liter, NaNO₃.

¹ The information presented here is the result of studies made at the University of Chicago. I wish to express warm thanks to Dr. W. C. Allee for his guidance in the prosecution of this work. I wish also to thank Mr. Asher J. Finkel for his help with the statistical analysis.

² Present address: University of Idaho, Moscow, Idaho.

Experiment I was the original experiment and was designed simply to find whether homosexual small groups have a social hierarchy.

Experiment II employed the fishes used in Experiment I, but they were assembled according to rank—i.e., all of the top-ranking fishes from the various aquaria in Experiment I were placed together in one aquarium for continued study. The same was done for the vari-

soon as hierarchies had become established, the most dominant individual in each aquarium was interchanged with the most dominant individual in another aquarium. Observations were made at the time of the transfer and for 30 minutes thereafter. Males and females were not mixed in this process. The exchange was made twice during the course of the experiment, and general observations were continued for almost 3 weeks. Ex-

TABLE I
MAKEUP OF THE VARIOUS EXPERIMENTS*

Experimental Conditions	Expt. I	Expt. II	Expt. III	Expt. IV	Expt. V
Location.....	W.L.	W.L.	W.L.	W.L.	W.L.G.
Type of water.....	a.p.	a.p.	a.p.	a.p.	tap
Temperature of water.....	75° F.†	75° F.†	75° F.†	75° F.†	variable
Lighting.....	L.F.	L.F.	L.F.	L.F.	daylight
No. of aquaria.....	8	8	6	8	1
Size of aquaria.....	30.5×26.5×26.5 cm.				8'×2'×1'3"
No. of fishes in aquarium.....	4	4	4	4	10
Origin of fishes.....	new	Expt. I	new	new	new
No. of aquaria containing ♀♀ only.....	4	4	0	4	0
No. of aquaria containing ♂♂ only.....	4	4	0	4	0
No. of aquaria containing equal numbers of ♂♂ and ♀♀.....	0	0	6	0	1
Duration in days.....	33	26	26	18	20
No. of days of observations made.....	20	15	20	16	10
Length of observation periods (in minutes)...	30	30	30	30	60

* W.L., Whitman Laboratory; W.L.G., Whitman Laboratory Greenhouse; a.p., artificial pond water; tap, tap water; L.F., Fluorescent and ordinary electric lights.

† Approximate temperature.

ous other ranks. The sexes were not mixed. The experiment was designed to find whether the top-ranking fishes were innately more aggressive or less social than those occupying lower positions in a hierarchy and whether they would establish rank orders as readily as did unselected groups.

Experiment III was designed to allow comparison between heterosexual and homosexual groupings. New fishes that had not been used in previous experiments were procured for the purpose.

At the beginning, Experiment IV duplicated Experiment I. However, as

periment IV tested the reactions of an established hierarchy toward a strange fish and the reactions of the strange fish to the new group.

Experiment V concerned territoriality. By using a fairly large tank containing plants and open water, it was hoped that a sufficient variety of conditions was present to allow the fishes to establish territories if such was their normal tendency.

DEFINITIONS

The term *nip* is used to designate the characteristic contact reaction between

two fishes. Essentially this is a quick bite, involving no noticeable harm to the fish that is bitten. Because *Platypoecilus* has a dorsally placed mouth, the nips tend to be directed upward and are received on the ventral part of the body. When possible, the nipped fish retreats upward in the most direct path of escape. A *nip* is analogous to a *peck* in the so-called "peck-order" studies with birds.

The term *challenge* refers to a characteristic type of behavior wherein a belligerent fish erects its dorsal fin, spreads its caudal fin, and fans the water with its pectoral fins. At the same time it bends its body into a shallow S-shape. The head is higher in the water than the tail.

The *submission* behavior in this species involves lowering of the dorsal fin, collapsing of the caudal fin, and a general drooping of the entire body. A submission reaction also involves backing slowly away for 2 or 3 inches. The animal then turns and flees.

Nip right is a form of dominance behavior in which one fish may nip another fish without being nipped in return.

Nip-dominance behavior, which does not occur in *Platypoecilus*, would involve steady reciprocal nipping but with one member of a contact-pair winning the majority of nip contacts.

A *contact-pair* is composed of any two fishes that have established, or are in the process of establishing, a dominance-subordination relationship.

FORMATION OF INITIAL HIERARCHIES

GROUPS OF FOUR FEMALES

When four *Platypoecilus* females are first brought together, each sinks to the bottom and indicates her alertness by erecting her dorsal and spreading her caudal fin. Each fish remains in this state for a few seconds or even several minutes.

Soon one individual becomes less alert, as indicated by the return of the dorsal and caudal fins to their usual positions. She begins to cruise slowly about until she encounters another fish. When the distance between the two fishes is approximately 2 inches, both exhibit challenging behavior. In this posture the two drift slowly until one turns suddenly upon the other and nips her. If nipping occurs, it will continue at intervals until the victim shows submission. Actually, the sequence seldom is completed at the first meeting. Indeed, the first encounter usually involves mutual challenging alone. In other instances an attack follows, but there is no noticeable submission by the victim. Under such circumstances the erstwhile aggressor may become the victim at the next meeting. A lasting dominance-subordination relationship is not visibly established until the victim submits to the aggressor without challenging by either fish.

While the first pair is reacting as a temporary contact-pair, the other two fishes usually exhibit similar behavior. Their series of meetings appears to be precisely similar to that of the first pair.

During the intervals between her aggressive meetings with a particular fish, an individual usually does not avoid the other fishes except when they are engaged in challenge reactions. Any encounters between lone fishes will result in challenging. As a result, all possible dominance-subordination relationships are usually established within a short time (about 30 minutes was the shortest time observed). An exception occurs when one fish is especially aggressive. Such an individual interferes actively with the contact-pair reactions of the others by attacking the challenger of a third fish. This aggressiveness results in the establishment of the nip order between the overly active individual and

the other three fishes before all of the other dominance-subordination relationships are settled. Under such circumstances, as many as 7 days may be required for the working-out of the complete social order.

GROUPS OF FOUR MALES

When a group of four *Platypoecilus* males is first assembled, the behavior of the individuals composing the group resembles that of females under the same conditions. The same social tension exists. There is the same mutual challenging and the same establishment of contact-pairs. However, certain differences are apparent almost immediately. The males tend to remain longer in one spot; their movements are more jerky and rapid; and their nipping appears to be more intense. Because the males tend to move only to challenge or to fight, while the females move about the aquarium almost continually, males meet in contact-pairs less frequently than do females, and more time is required for their social order to be worked out. The least time observed for the formation of a complete set of relationships among four males was 1 day; the greatest, 12 days.

Male dominance-subordination relationships tend to be established one at a time rather than more or less simultaneously, as with females. Thus, each of the first two contact-pairs in a newly established group of males may continue with an extended series of contact reactions until their dominance-subordination relationship is fully determined. Usually, the two original contact-pairs do not break up, nor are new contact-pairs formed until this has happened.

One of the two original contact-pairs frequently establishes its dominance subordination relationship before the other. Its members then separate, and one or both may interfere with the

other initial pair by challenging or attacking either of its members. Such behavior may disrupt this pair, for one of them may react to the new challenge instead of the original one. Under these conditions the two original contact-pairs may not be the first to establish their relationships.

HETEROSEXUAL GROUPS

Taken as a whole, the general behavior of a group of *Platypoecilus* consisting of two males and two females has much in common with that of homosexual groups of four fishes. The initial period is much like that of a homosexual female group in that the fishes are rather steadily on the move. The males swim about much more than in male homosexual groups; but they move in a jerky manner, in contrast to the smoother swimming of the females. No breeding behavior was noted during the formative period in any of the six aquaria observed in Experiment III. The establishment of dominance-subordination relationships tends to follow the male, rather than the female, pattern; and the males tend to occupy the more dominant positions in the group, even at the beginning of its social history. This was true in five of the six aquaria involved in the experiment.

HIERARCHY TYPES AND THEIR DISTRIBUTION

The establishment of a set of dominance-subordination relationships for contact-pairs automatically results in the establishment of a hierarchy. Frequently this will be a *true straight-line* hierarchy, in which each individual dominates all others whose rank is lower than its own. This may be considered the completion of the social integration of the group. Such hierarchies were observed many times.

It is not uncommon to observe a set of

nip relationships in which the contact-pairs are not all formed or are of such a nature that it is impossible to recognize a complete hierarchy. Overtly, these incomplete hierarchies are of two types: a *pseudo-straight-line* hierarchy, one in which no fish is out of line but each fish does not nip all individuals whose rank is lower than its own, and an *incomplete*

TABLE 2
TYPES OF HIERARCHIES

Type of Hierarchy	No. of Fishes Dominated	Individuals Dominated
I. True straight-line:		
B.	3	D.C.A.
D.	2	C.A.
C.	1	A.
A.	0	
II. Pseudo-straight-line:		
B.	3	A.C.D.
D.	1	C.
C.	1	A.
A.	0	
III. Incomplete proper:		
B.	3	A.C.D.
C.	2	A. D.
A.	0	
D.	0	
IV. Non-straight-line:		
D.	2	A.C.
A.	2	C.B.
B.	1	D.
C.	0	

hierarchy proper, one in which the position of one or more individuals is undetermined. Apparently, the incomplete types do not differ in kind from the true straight-line hierarchy, but they occur frequently enough to justify naming them. These are illustrated in Table 2 by different stages in the evolution of the final social order in aquarium No. 1 of Experiment I.

Not all hierarchies are of the straight-

line type. In some, one or more individuals are out of line. This is analogous to the triangle situation as seen in chickens. I have chosen the term *non-straight-line hierarchy* to describe a social grouping of this type. The example given in Table 2 is from aquarium No. 4 of Experiment II.

The true straight-line hierarchy occurs when there is not too great a difference between the belligerency of the individuals. The incomplete types occur most frequently when one individual, usually the most dominant fish, attacks the other fishes so steadily that they are unable to work out all their interrelationships. It is also possible that in some cases the relationships have been worked out, but the dominant fish does not permit the less aggressive individuals to exercise them. The non-straight-line hierarchy can be explained at this time only on the postulate that the fishes recognize each other as individuals, as do hens (Schjelderup-Ebbe, 1922).

The distribution of the various hierarchy types seems to differ in the different sexual arrangements. Differences of equal magnitude may be noted between aquaria containing groups of similar sexual composition. The figures presented in Table 3 are totals which may show a trend in distribution and are offered for what they may be worth. It may well be that factors other than sex are the major determiners of the type of hierarchy. On the basis of Table 3, true straight-line hierarchies are most likely to occur in homosexual female groups and least likely to occur in heterosexual groups. Pseudo-straight-line hierarchies have about the same frequency in each of the three groupings. Incomplete hierarchies proper are most common in heterosexual groups and least common in homosexual male groups. Non-straight-line types occur most frequently in male

homosexual groups, least frequently in female homosexual groups.

THE EXISTENCE OF NIP RIGHT

The dominance relationship upon which the hierarchies are based is of the nip-right type; i.e., any despot has the right to nip its subordinates but is not normally nipped by them. This phenomenon is not quite so apparent here as is peck right in the case of chickens. The slight obscurity results from the instability of the hierarchies. Reverse nipping occurs but constitutes a very small per-

centage of individuals that are characteristic of individuals that are strange to each other. Under the influence of an established society the fishes move about freely. There is little challenging, and such as does occur indicates attempted revolts by subordinates. Most challenging evokes an immediate attack by the challenged despot, with the result that there is little mutual challenging. Nipping in an established hierarchy appears to be less intense than in the formative period except when a despot is thwarting an attempted revolt. Any despot may interfere with the contact-

TABLE 3
DISTRIBUTION OF HIERARCHY TYPES (FOUR FISHES)

TYPE OF HIERARCHY	FEMALES (EXPT. I)		MALES (EXPT. II)		HETEROSEXUAL GROUPS (EXPT. III)	
	No. of Daily Hierarchies	Percentage	No. of Daily Hierarchies	Percentage	No. of Daily Hierarchies	Percentage
True straight-line. . .	43	53.8	32	40.0	23	18.3
Pseudo-straight-line. .	11	13.8	12	15.0	17	13.5
Incomplete proper. . .	20	25.0	16	20.0	72	57.2
Non-straight-line. . .	6	7.5	20	25.0	14	11.1

centage of the total amount of nipping done (Table 4). Also, reverse nipping is intermittent, not continuous, and thus represents either accidental nipping resulting perhaps from lack of recognition of a more dominant fish or else an attempted revolt against a despot. Until further data are available, it is not clear what significance underlies the observed differences in reverse nipping in the different combinations.

BEHAVIOR IN ESTABLISHED HIERARCHIES

GROUPS OF FOUR FEMALES

The behavior of *Platyopocilus* females after a hierarchy has become established differs somewhat from that shown earlier. There is a lack of the social tension so

pair relationships of her subordinates and break them up by nipping either of the fishes involved.

The females are not uniformly active but alternate between relatively long periods of activity and relatively shorter ones of inactivity. General inactivity is initiated when any one of the four individuals enters a secluded portion of the aquarium and remains there. Soon a second fish will settle down in another secluded spot or corner or will come to rest upon the bottom of the aquarium. This process continues until all four fishes have become quiet. During the inactive period that ensues the individual fishes may move about, one at a time, but their movements are slow, and they avoid the vicinity of others.

An inactive period ends when any one of the four fishes begins to move about the aquarium rapidly and nip her subordinates when she encounters them. The nipped animals swim on actively and may nip their own subordinates. Thus in a few seconds the four fishes may proceed from the inactive to an extremely active phase of their social behavior.

GROUPS OF FOUR MALES

After a hierarchy has become established, the behavior of *Platypoecilus* males does not change so much as it does in a group of females. Social tensions

TABLE 4

DISTRIBUTION OF REVERSE NIPPING
EXPERIMENTS I AND III

Grouping	Percentage of Reverse Nipping	Total No. of Nips
Homosexual:		
Females nip females.....	0.8	13,059
Males nip males.....	2.4	9,355
Heterosexual:		
Females nip females.....	1.4	1,984
Males nip males.....	0.3	3,495
Nips between males and females.....	0.8	5,766

persist; the same jerky movements and intense nipping may be observed. However, challenging—especially mutual challenging—is infrequent. As before, males tend to move about less frequently and with less smoothness of motion than the females exhibit at a comparable stage in group life.

The alternating periods of inactivity and activity noted for the females have their counterpart in the male groupings, but the inactive periods of the males are proportionately longer. Social activity is characterized by a series of events such as occurs with the females, but the male activity is more intense throughout.

During periods of inactivity, even

when the males are not engaged in contact-pair reactions, their postures indicate alertness. In this they differ from the females, which seem to be completely at rest during their period of social quiet.

Male nipping is generally more vigorous than female nipping, but males do less nipping than the females. In Experiment I the females averaged 81.6 nips, while the males averaged only 58.5 nips, per fish per hour.

HETEROSEXUAL GROUPS OF TWO MALES AND TWO FEMALES

The behavior of the fishes in an established heterosexual group resembles that shown by a homosexual group of females. Fishes of both sexes move about the aquarium rather steadily during any active period. The relatively greater activity of the males, as compared with that in male homosexual groups, is notable and may well be related to the presence of the females, which move about in their normal manner and thus keep the males in motion. The stimulus furnished by the females is social rather than primarily sexual, for the females keep the males in motion even during periods when no breeding activity can be noted. The jerkiness of movement of the males is not quite so noticeable as it is under homosexual circumstances. Periods of inactivity occur here, as elsewhere; they are relatively less frequent than in groups of males and no more frequent than in groups of females. Challenging is infrequent and commonly indicates an attempted revolt.

Males nip individuals of both sexes, and females do the same (Table 5). Males and females divide their nipping rather equally between the sexes except during breeding periods, when males mainly nip other males. During such periods a male will follow a sexually receptive female and attempt to mate with

her. If the female challenges, as she often will, the male may nip her, but rarely otherwise. In half of the aquaria in Experiment III the females gave the majority of their nips to other females; in the other half, males received more of the nips given by their associated females.

TABLE 5
HETEROSEXUAL GROUPS, EXPERIMENT III
DISTRIBUTION OF NIPPING
ACCORDING TO SEX

Sexual Combinations	Total No. of Nips	Percentage
Male nips male.....	3,495	31.1
Male nips female.....	3,327	29.6
Female nips female.....	1,983	17.6
Female nips male.....	2,439	21.7

In heterosexual groups males nip more than do females—approximately 54.1 nips per fish per hour as contrasted with 35 nips for females. This is in sharp contrast to the situation in male and female homosexual groups, where the females do more nipping. Examination indicates that we are here dealing with a decrease in the female nipping rate rather than an increase in that of the males. No explanation for this fact is offered at this time except the possibility that the sometimes severe nipping of the males causes the females to spend more time escaping from them and less time in aggressive behavior toward other fishes. The greater intensity of male nipping gives them a social advantage in heterosexual groups. This is expressed as a strong tendency for males to be despots in such groups (Table 6).

SOME ELEMENTS OF SOCIAL BEHAVIOR IN ESTABLISHED GROUPS

Within the framework of a true straight-line hierarchy there is a steady downward progression in the amount of nipping done by fishes occupying the

several ranks. This is generally true for homosexual groups of both sexes and for heterosexual groups as well (Table 7). Thus the amount of nipping done by any individual corresponds to the position of that individual in the hierarchy.

This was true for each of the four aquaria containing females in Experiment I and for three of the four aquaria containing males. In the fourth aquarium the score was 142 nips for the No. 1 rank, against 163 for the No. 2. In the heterosexual groupings of Experiment III the amount of nipping corresponded to rank in five of the six aquaria used, while in the sixth the No. 1 and No. 2 positions were precisely equal, with 65 nips apiece. In both aquaria where the differences were out of line with the general trend the amount of nipping was at a minimum.

A despot does not distribute its nipping evenly among its subordinates, nor does it always nip its subordinates according to rank. Rather, the despot nips

TABLE 6
HETEROSEXUAL GROUPS, EXPERIMENT III: DIS-
TRIBUTION OF NO. 1 RANK IN TRUE
STRAIGHT-LINE HIERARCHIES

Aquarium No.	Days Males Held Top Rank	Days Females Held Top Rank
1.....	21	0
2.....	18	3
3.....	12	2
4.....	1	7
5.....	4	8
6.....	5	6
Totals.....	60 (69.8%)	26 (30.2%)

each individual subordinate differentially (Tables 8, 9, and 10).

The rank of the fish most likely to receive the majority of the nips given by a superior fish varies from aquarium to aquarium, regardless of the type of sexual grouping used (Table 8) and regard-

less of whether the nips of the alpha or beta fish are used in the analysis (Table 9).

Marked differential nipping is received by different individuals (Table 10). The

least in part—from the recognition of, and reaction to, individuals as such.

The stability of any hierarchy is a function of the stabilities of the various subrelationships within the hierarchy,

TABLE 7

AMOUNT OF NIPPING DONE BY THE FISHES OCCUPYING EACH OF THE FOUR POSITIONS
IN TRUE STRAIGHT-LINE HIERARCHIES

SEX	EXPT.	No. 1 FISH		No. 2 FISH		No. 3 FISH		No. 4 FISH	
		Nips	Per Cent	Nips	Per Cent	Nips	Per Cent	Nips	Per Cent
Females.....	I	4,886	63.5	2,292	28.9	481	6.3	31	0.4
Males.....	I	2,214	59.7	1,168	31.5	309	8.3	16	0.4
Heterosexual.....	III	1,505	59.7	808	32.0	202	8.0	5	0.2

TABLE 8

TRUE STRAIGHT-LINE HIERARCHIES: DISTRIBUTION OF NIPPING BY THE NO. 1 FISH

AQUARIUM NO.	NO. 2 FISH	NO. 3 FISH	NO. 4 FISH
Females, Experiment I			
1.....	655	379	383
2.....	474	555	377
3.....	492	246	443
4.....	249	422	342
Males, Experiment I			
5.....	41	163	31
6.....	129	7	6
7.....	219	317	306
8.....	274	627	94
Heterosexual, Experiment III			
1.....	159	117	107
2.....	30	9	26
3.....	7	4	18
4.....	103	24	87
5.....	36	114	167
6.....	356	103	53

evidence given in Tables 8 and 9 indicates that this is not directly related to differences in rank; it may result—at

such as the length of time one fish can dominate one, two, or three others. As would be expected, considering the instability of the hierarchies, such subrelationships are usually short-lived; in fact, the greater number of cases observed endured only for 1 day (Table 11). It should be noted that instability may not be a fundamental characteristic of *Platy-poecilus* societies at all times and under all conditions. Further work may show that the size of the aquarium is a factor in stability. Also, long-term observations may provide evidence of an increasing stability as time passes. Reference to Table 11 will show that the relationships of certain individuals were of exceptionally long duration. There were 11 cases among the females of Experiment I in which one female dominated another for 29 days—the entire observation period for that experiment. Similarly, in the same experiment there were 5 cases wherein one female succeeded in dominating two others for 29 days. While these cases and similar ones among the males (Expt. I) and the heterosexual grouping (Expt. III) may be regarded as exceptional under the conditions of these experiments, they constitute evidence

that stability is possible. The factors making for stability are, at present, unknown.

The differences between the mean durations of each of the subrelationships (Table 11) were tested for statistical significance; none was found. Unless the lack of statistical significance can be attributed to the small number of cases tested or to an unrepresentative sample, it appears that the more complicated relationships are as likely to endure as the less complicated ones; i.e., one fish can dominate two or three others as easily as one. This would be evidence for individual recognition.

Wholly similar comparative studies were made of the durations of the subrelationships between homosexual male, homosexual female, and heterosexual groupings; this was done statistically by testing the mean differences for significance. None was discovered for the more complicated relationships, possibly because of the small number of cases involved. However, in all cases the male homosexual and heterosexual durations were shorter than those of the homosexual female grouping—significantly so for one male dominating one of two individuals. No significant differences were noted between the male homosexual and the heterosexual relationships.⁴

Changes in rank occur frequently among these fishes within any hierarchy, and the frequency of such changes is a measure of the instability of the relationships. Such changes result from successful revolts and are characterized by a period or a succession of periods of mutual challenging lasting from a few seconds to as long as 30 minutes. Mutual challenging appears to be an outward sign of a pe-

riod of temporary equality between the members of the contact-pair involved, since a truly dominant fish will attack its subordinate without challenging it. Most of the observed revolts involved the reversal of only one contact-pair relationship. However, a fish that has overthrown one of its despots may continue its course

TABLE 9

TRUE STRAIGHT-LINE HIERARCHIES: DISTRIBUTION OF NIPPING BY THE NO. 2 FISH

AQUARIUM No.	No. 3 FISH	No. 4 FISH
Females, Experiment I		
1.....	1,277	533
2.....	520	281
3.....	630	159
4.....	22	100
Males, Experiment I		
5.....	117	17
6.....	42	120
7.....	352	387
8.....	54	71
Heterosexual, Experiment III		
1.....	40	151
2.....	60	5
3.....	26	1
4.....	61	5
5.....	30	130
6.....	112	79

of self-emancipation until it has overthrown a second or even a third despot. This disruptive behavior may create such chaos in the aquarium that contact relationships between other individuals will be reversed.⁵ The foregoing account holds

⁵ Aquarium No. 2, Expt. I, ♀ ♀, March 2-3. The hierarchy changed from D-B-C-A to A-B-D-C. Thus, contact pairs AB, AD, and BD were reversed.

Aquarium No. 3, Expt. I, ♀ ♀, February 17-20. The hierarchy changed from D-C-B-A to A-D-C-B. Thus, AB, AC, and AD were reversed.

⁴ Detailed data have been recorded elsewhere (Braddock, 1942) in a form similar to that shown in Table 11, and only the respective means are given here.

good for all of the sexual groupings observed. However, revolts are most likely to affect more than one contact-pair in the case of homosexual female groups (44 per cent) and least likely to do so in homosexual male groups (28 per cent). Heterosexual groups resemble the fe-

stability than reverse nipping, since the latter may occur by accident or in connection with unsuccessful revolts. At present there is insufficient evidence to determine which, if any, of the several subordinate ranks is most likely to overthrow a despot.

TABLE 10
DIFFERENTIAL NIPPING ACCORDING TO INDIVIDUAL FISHES

AQUARIUM No.	A-B	A-C	A-D	B-A	B-C	B-D	C-A	C-B	C-D	D-A	D-B	D-C
Females, Experiment I												
1.....	0	0	10	789	434	1,293	496	510	178	17	0	57
2.....	66	13	38	294	362	152	166	0	0	581	613	1,134
3.....	1	16	152	181	3	0	229	991	1	468	291	642
4.....	27	117	0	1	132	0	0	0	0	778	866	960
Males, Experiment I												
5.....	201	4	17	89	703	36	148	1	154	40	46	523
6.....	298	25	25	24	0	388	276	1,254	3	39	10	588
7.....	59	0	0	45	0	26	683	201	90	328	640	214
8.....	0	90	159	466	1,064	120	6	0	213	0	50	25
Heterosexual, Experiment III												
1.....	5	0	1	4	1	0	634	481	476	152	390	0
2.....	9	5	1	47	8	13	482	18	0	267	95	412
3.....	450	17	4	0	5	0	0	7	0	40	131	468
4.....	677	563	30	58	157	58	5	44	828	203	8	0
5.....	2	130	32	431	754	19	8	0	7	58	14	312
6.....	299	531	76	2	10	24	17	123	713	34	116	159

male homosexual groupings in this respect (42 per cent).

The frequency of successful revolts in each of the sexual groupings may be used as an index to the relative stabilities of the groupings. On this basis the female homosexual groups are the most stable. The male homosexual and heterosexual groupings are approximately equal to each other in stability, but both are less stable than the females.⁶ Successful revolts constitute a better index of relative

HOMOSEXUAL GROUPS SELECTED ACCORD-
ING TO THEIR SEVERAL RANKS
IN EXPERIMENT I

Experiment II was designed to test the importance of general aggressiveness in hierarchy formation and maintenance. In each aquarium in Experiment I one individual held the No. 1 position for a greater number of days than any other fish. The same was true for each of the other three positions. On this basis it was

⁶ Relative numbers of successful revolts: ♀♀, homosexual groups, 0.061 revolts per fish per day;

♂♂, homosexual groups, 0.118 revolts per fish per day; and heterosexual groups, 0.132 revolts per fish per day.

possible, at the conclusion of Experiment I, to designate each fish as a No. 1, 2, 3, or 4 individual.

In Experiment II all of the No. 1 females were assembled in one aquarium. All of the No. 2 females were placed in another aquarium. The same was done for the females of the other ranks and

(Table 12). The amount of reverse nipping increased from 0.8 per cent for females selected at random to 1.8 per cent for females selected for rank. The males showed a similar increase (2.4-4.3 per cent). These data are given with some reserve; yet the indicated trend may be real.

TABLE 11

EXPERIMENT I: DISTRIBUTION OF DURATION OF VARIOUS DOMINANCE RELATIONSHIPS FOR FEMALES, TOGETHER WITH MEANS FOR SIMILAR DATA FOR MALES AND FOR BISEXUAL GROUPS

Duration in Days	One Fish Dominates One Other	One Fish Dominates Two Others	One Fish Dominates Three Others	Three Fishes Maintain Same Hierarchy	Four Fishes Maintain Same Hierarchy
No. of cases	63	47	13	79	35
Duration in days					
1	38.1%	36.2%	30.8%	48.1%	62.9%
2	4.7	2.1		8.9	17.1
3	3.2	6.4	7.7	3.8	5.7
4	3.2	4.3	7.7	6.3	5.7
5	1.6			3.8	2.9
6	6.3	4.3		8.9	2.9
7				2.5	2.9
8	6.3	8.5	15.4	7.6	
9		4.3	7.7	1.3	
10				1.3	
11	6.3	12.8	15.4	3.8	
12				1.3	
13	1.6				
14	1.6	2.1		1.3	
15	1.6	2.1			
16	1.6	4.3	7.7		
18			7.7		
22				1.3	
23	4.7	2.1			
26	1.6				
29	17.5	10.6			
Totals	99.9	100.1	100.1	100.2	100.1
Mean, females	9.9 days	8.4 days	7.1 days	3.8 days	1.9 days
Mean, males	5.8	4.3	3.2	2.9	1.5
Mean, bisexual	5.0	4.4	3.9	2.3	1.2

for the males. Thus, Experiment II exactly duplicated Experiment I with the single exception that an attempt was made to place together individuals of a similar degree of aggressiveness.

The results were not a duplication of those of Experiment I. True straight-line hierarchies were rarer both for males and females selected for rank, and incomplete hierarchies were more common

The total amount of nipping underwent a decrease from 81.6 to 47.9 nips per fish per hour for females and from 58.5 to 24.4 nips per fish per hour for males selected for rank.

As was to be expected, the several subrelationships tended to be short-lived, the greatest number of examples lasting only 1 day (Table 13). In the case of the females the mean duration of

the time one fish dominated one other or one fish dominated two others was significantly shorter for fishes selected for rank. The males showed no significant differences for any of the relationships.

The above information tends to indicate that general aggressiveness is important and that groups composed of individuals with a similar degree of this quality have more difficulty in forming

factor in dominance behavior among these fishes, but in the early weeks of a given group relationship it is more important than the rank held at the moment.

TRANSFERS TO ESTABLISHED HIERARCHIES

Experiment IV was designed to study the reactions of a fish newly introduced

TABLE 12

DISTRIBUTION OF HIERARCHY TYPES: MALES AND FEMALES, EXPERIMENT II

HIERARCHY TYPES	FEMALES		MALES	
	No. of Daily Hierarchies	Percentage	No. of Daily Hierarchies	Percentage
True straight-line.....	15	27.8	7	13.0
Pseudo-straight-line.....	9	16.7	14	25.9
Incomplete proper.....	25	46.3	23	42.6
Non-straight-line.....	5	9.3	10	18.5

TABLE 13

DISTRIBUTION OF DURATIONS OF VARIOUS DOMINANCE RELATIONSHIPS
MALES AND FEMALES, EXPERIMENT II

DOMINANCE RELATION	FEMALES		MALES	
	No. of Cases	Mean	No. of Cases	Mean
One fish dominates one fish.....	66	6.3	79	4.5
One fish dominates two fishes.....	47	4.9	59	2.5
One fish dominates three fishes.....	12	4.3	12	1.7
Three fishes maintain same hierarchy.....	61	2.5	51	2.2
Four fishes maintain same hierarchy.....	22	1.5	27	1.1

and maintaining hierarchies than do groups selected at random. It seems logical that any two fishes that are almost equally aggressive will have more difficulty in establishing and maintaining a stable dominance-subordination relationship than two with much variation in aggressiveness. This is reflected throughout the whole hierarchy. It is not suggested that general aggressiveness is the only

into an established hierarchy and the reactions of the original members of the hierarchy to the stranger. Otherwise the experimental setup situation duplicated that of Experiment I—i.e., homosexual groupings of four fishes with four aquaria for each sex. After the original groups had been together long enough to make possible the ranking of the individuals by the method used in Experiment II—

i.e., by customary rank rather than rank at the moment—the fish that was usually No. 1 was removed from each aquarium and placed in another; all were No. 1 or No. 2 fishes on the basis of rank at the moment of transfer. The number of individuals in each aquarium remained the same, but there was a stranger in each group. The sexes were not mixed in making the transfers. Observations were made for the 30-minute period immediately following the exchange or for a longer time, if necessary, and for the regular half-hour periods on succeeding days. After these new groupings had established their hierarchies, a similar rearrangement was made, and a second set of observations was recorded.

Under the above conditions an individual newly introduced into an established hierarchy invariably exhibited submissive reactions to any fish approaching it. The resident fishes attacked the stranger almost immediately. In all but 2 cases the highest-ranking fish attacked first, followed by the others—not necessarily in the order of their rank. No challenging was observed—an indication that the fishes native to the aquarium recognized their advantage over the new fish. The behavior during this initial period was essentially the same for male and female groups.

Shortly after the initial period of submission the foreign individual began to challenge the members of the established order. For males the minimum time that elapsed before this happened was 5 minutes; with females the minimum time was more than 30 minutes. The maxima were 28 minutes for males and 2 days for females. From then on the new fish established its relationships with the other fishes one by one and finally achieved a position in the hierarchy above the omega one occupied when first introduced.

TERRITORIES

Territoriality has been reported for birds in connection with peck-order studies in the case of ring doves (Bennett, 1939), geese (Jenkins, 1944), canaries (Shoemaker, 1939), and others and for some of the nest-guarding fishes (Breder, 1936; Noble and Curtis, 1939). Noble and Curtis (1939) have reported the existence of breeding territories in the cyclid *Hemichromis bimaculatus*. The phenomenon has not been observed in any of the live-bearing fishes. The association between territoriality and *peck-dominance* rather than *peck-right* organization has been summarized by Allee (1942).

The large tank employed in Experiment V had plants at both ends and a clear space in the middle. It was believed that enough variety of environment existed to permit the fishes to find suitable territories if it were their nature to do so. Only ten individuals—five males and five females—were used, in order that the fishes could avoid each other and thus have an opportunity to take over territories without undue interference.

No evidence of territorial behavior was noted in Experiment V. The fishes tended to school into a loosely integrated group; and, so far as could be observed, the contact-pair relationships were the same on a given day anywhere in the aquarium. There has been no evidence of territoriality in any of the other observations.

THE PROBLEM OF INDIVIDUAL RECOGNITION

There is little exact evidence in this work that bears on the problem of the possible individual recognition of one fish by another. There are two lines of available evidence. One of these lies in the frequency of differential nipping of sub-

ordinate fishes by the common despot, regardless of rank in the hierarchy. Differential nipping may indicate individual recognition, or it may result from differential reaction to differing behavior patterns without actual recognition of associated fishes as individuals. Thus, any fish that gives a reaction approaching a "challenge" is nipped by its despot, and the No. 3 fish may give such reactions more than the individual in the No. 2 position. The despot may then react to this tendency, not to the individual as such.

A second line of evidence comes from the existence of non-straight-line hierarchies. Such arrangements are marked by a high-ranking individual being regularly nipped by a fish that occupies a generally low position in the social order. In other words, nipping triangles or even quadrangles may exist in place of a straight-line order. If the outcome of pair contacts depended on chance alone, 25 per cent of all hierarchies in groups of three fishes should be of the non-straight-line type.⁷ Actually, about 9 per cent of 640 hierarchies were of this sort.

When four fish are considered, if all pair contacts were won as a result of chance, 62.5 per cent of the hierarchies would be non-straight-line. Actually, about 16 per cent of 160 observed hierarchies were of this kind. The strong indications are that the outcome of these pair contacts is not a matter of chance; and, although non-straight-line hierarchies suggest individual recognition, it seems likely that this is only one of a number of factors acting in the establishment and maintenance of social ranks in *Platyopocilus*. Finally, the series of

events following the introduction of a strange fish into an established hierarchy may give some evidence of individual recognition. While the foreign fish may well be reacting to the strangeness of its new environment and to the threatening behavior of a whole set of fishes, rather than to its new associates as strange individuals, there seems to be little doubt that the resident fishes are reacting to the introduced fish as an individual whose strangeness is detected.

FACTORS INVOLVED IN DOMINANCE

It is not a simple matter to account for dominance in specific terms. There is evidence that dominance is the result of intricately interwoven qualities, some of which are at present unknown. Furthermore, in fishes the relative importance of the various known factors has not been determined.

Perhaps general aggressiveness itself is the most important single factor known to help determine the dominance potential of an individual; yet aggressiveness is a complex as yet unanalyzed for any animal. It seems probable that future work will break this composite down into more basic factors and discover the role played in aggressiveness by such factors as size, sex, and certain psychological considerations, together with others as yet unknown. At present the only objective measure known for aggressiveness in these fishes is that furnished by nipping. Certainly there exists a close correspondence between an individual's capacity for dominating others and the amount of nipping done by that individual over a period of time. It has been shown (Table 7) that a more dominant fish will do more nipping than a less dominant fish. Furthermore, the data on amount of nipping, and on the number of days each fish dominated each other fish in Experiments I, II, and III were tested

⁷ The number of possible straight-line hierarchies is indicated by factorial $n(n!)$, where n is the number of individuals present. The total number of different kinds of ranked arrangements of individuals is $2[n(n-1)/2]$. I am indebted to Professor Sewall Wright for these formulas.

for correlation. The r -values are given in Table 14, and they indicate a fairly close correlation. If there were no interrelationship between amount of nipping and dominance, such a close correlation would be most unlikely. For instance, A might be despot over B for 10 days and

TABLE 14

CORRELATION BETWEEN HIGH RATE OF
NIPPING AND DOMINANCE

Expt.	Sex	r
I.	Females	0.894
I.	Males	0.893
II.	Females	0.74
II.	Males	0.82
III.	Heterosexual	0.73

nip B 500 times during that period; after a reversal that resulted in B becoming despot over A, B might then dominate A for 5 days and nip A 1,000 times over that period. Such examples have not been observed. The foregoing evidence indicates that a close interrelationship exists between dominance and the amount of nipping done.

The next question is whether nipping is a privilege conferred by dominance and having no significance yet noted or whether it is an instrument of social control. By "social control" is meant the maintenance of hierarchy stability through stability of the several contact-pair relationships. While the answer to this question is not as yet entirely clear, there are indications that the latter alternative is the more probable. The homosexual female groupings combine the highest nipping rate with the highest measure of hierarchy stability observed in these experiments. The homosexual male groupings exhibit less nipping and less stability. Thus, it is suggested that constant nipping by a despot may tend to discourage revolts and thus maintain the dominant position of the despot. If

this is true, we can conclude that aggressiveness produces nipping, which is one factor in the initiation and maintenance of dominance.⁸

Another factor is size (Table 15). The available data present no exact, over-all correlation between size and dominance because the actual size of each fish was not measured. (The less one handles these fishes, the healthier they remain.) However, the various pair combinations were analyzed to find what percentage of the time the fish judged to be larger dominated a smaller one. There are indications that, under random conditions, size is a more important factor for males than for females. This is true whether the males are in homosexual groupings with other males (Expt. I) or in heterosexual groupings with females (Expt. III). In the case of contact relationships between males and females, size is less

TABLE 15

FREQUENCY WITH WHICH THE LARGER OF
TWO FISHES DOMINATED THE
SMALLER FISH

Expt.	Sexual Grouping	Percentage of Larger Fish Dominated
I.	{ Females, homosexual Males, homosexual	50.6 69.7
II.	{ Females, homosexual Males, homosexual	72.6 58.8
III.	{ Heterosexual, all cases Females and females Males and males Males and females	62.2 57.6 71.0 58.0

important than in unisexual lots of males and somewhat more important than in unisexual female groups. When the fishes were grouped according to rank previously obtained (Expt. II),

⁸ The other possibility, i.e., that fishes nip because they are dominant, must not be neglected. If this is correct, the role of nipping in social life is undetermined.

indications were that the importance of size as a dominance factor was increased for the females and decreased for the males. Actually, size was now a more important factor for the females than for the males. The increase in the importance of size for females selected for rank seems to be a result of the process of selection which tended to equalize factors other than size but not size itself, since size is unimportant for females under random conditions. Thus, females selected for rank could still have much variation for size, and it could be emphasized beyond its usual importance. Males selected by the same process would tend to be more similar in size, and inequalities in other factors would receive the emphasis.

That maleness is a factor in dominance is demonstrated by the fact that 69.8 per cent of the No. 1 fishes in true straight-line hierarchies of four fishes (two males and two females) were males. This should be considered in connection with the fact that nipping is at its lowest level as a dominance factor under heterosexual conditions and that size is also relatively unimportant.

Psychological factors also enter the picture. The fact that a foreign fish submits without challenging when placed with fishes whose hierarchy is established brings this out. The nature of these psychological factors remains to be discovered.

There is no doubt but that there are other undiscovered qualities in the dominance potential; for there are occasional cases on record where a female fish dominated a male fish that was larger than herself and did more nipping. It is probable also that differential nipping, as applied to individual recognition and even aggressiveness, should be included among the psychological factors. In summary, the dominance potential is a re-

sult of aggressiveness; objectively considered, it is related to nipping, size, maleness, and psychological factors, together with many unknowns. A fish does not have to exceed another in all of the values that together constitute its dominance potential in order to occupy high social rank. It may be comparatively deficient in one or more of the measurable factors and still dominate another, probably because it has the advantage in the more crucial attributes that make for dominance.

DISCUSSION

In a general way the social behavior of *Platypoecilus* resembles that of chickens, as reported by Schjelderup-Ebbe (1922), Allee (1943), and others. Nip right appears to be analogous to peck right and is established in the same manner, i.e., by fighting or by passive submission. True straight-line hierarchies are characteristic of chickens, and the triangle situation is one form of non-straight-line hierarchy. There is much evidence that chickens maintain their relationships upon a basis of individual recognition; and the same appears to hold, at least in part, for the fishes studied here. Such differences as have been noted are quantitative. Among the fishes, non-straight-line hierarchies occur more frequently, and triangles and incomplete hierarchies are more characteristic. However, there is a strong tendency toward the straight-line relationship. This is apparent when one considers that non-straight-line relationships do not appear as frequently as they would if chance alone determined the outcome of all contact reactions. When the special conditions under which these observations were made are considered, the stability of *Platypoecilus* societies is definitely less than that of similar societies of hens. Groups of seven or eight hens may maintain the same rela-

tive positions for several months, while a day or two is the usual limit for *Platy-poecilus*. However, it should be noted that a few of the contact relationships observed lasted 29 days; this indicates that such relationships may have stability under special circumstances.

Noble (1939) reported what is here called *nip right* in the poecilid fish, *Xiphophorus helleri*; and his descriptions would fit, in a general way, the nip behavior of *Platy-poecilus*. This is to be expected, since the two interbreed freely and are similar in their general habits. Differences between the behavior of *Xiphophorus* as reported by Noble and that of *Platy-poecilus* are largely differences in the stability of the hierarchies. Noble states that the nip order of a "small school" of *Xiphophorus* may remain constant for 2 or 3 weeks. While individual contact-pair relationships among *Platy-poecilus* fishes have been known to last as long as 29 days, this was by no means characteristic of them and is still less so for hierarchies of four fishes. It seems possible that Noble's observations were made under different conditions from those reported here. It is not clear whether Noble began his observations immediately after the fishes were placed together or waited for some time before beginning observations. Thus, Noble's results may represent the situation present after the fishes have been together for a considerable time. Until observations designed to clarify this point have undergone analysis, this must remain an open question. Noble also reports a much stronger tendency toward the true straight-line hierarchy than was noted for *Platy-poecilus*. This may also result from differences in the conditions under which the two sets of observations were taken.

The problem of the value of dominance-based societies to their own mem-

bers and to the species at large is far from solved, but it has been ably discussed by other investigators (Allee, 1943; Collias, 1944; Noble, 1939). Noble adopted the point of view that dominance behavior is primarily concerned with natural selection of individuals. Allee (1938) and Collias (1944) also recognize the possibility of individual selection and, in addition, advance the hypothesis that hierarchies based on individual-against-individual competition may lead to the selection of the whole organized group in competition with other groups. It seems likely that both types of selection are important but under slightly different conditions.

That the survival potential of the whole group may be increased by dominance behavior is suggested by the following lines of evidence. Allee and Guhl (1942) have reported that hens in organized groups gain more weight, eat more, and lay more eggs than those in unorganized flocks. Taken in connection with the fact that fishes are most vulnerable to predators when very young, evidence that very young *Xiphophorus* have nip orders (Noble, 1939) seems significant. *Xiphophorus* adults do not protect their young in any way. Cyclid fishes protect their young; and, when thus protected, the young fishes are not organized into hierarchies (Noble and Curtis, 1939). However, if young cyclids are separated from their parents, they immediately develop social orders (Noble and Curtis, 1939), perhaps as a substitute for parental care. Adult cyclids, pugnacious fighters, do not exhibit dominance behavior (Noble and Curtis, 1939). Male *Bettas* also have no dominance-based societies (Noble, 1939); they, too, are noted for their pugnacity. Female *Bettas* are less pugnacious than males and have social orders (Noble, 1939). Male *Platy-poecilus* are more pugnacious

than females and have less stable social orders. While it is entirely possible that the evidence for fishes merely indicates that the more pugnacious types have less ability to form hierarchies, it is also possible that social groups are an alternative to ability for self-protection. As such they would protect the group as a whole rather than any particular individual in the group.

Evidence also exists that a dominant position within a group is correlated with a greater individual survival potential (Allee, 1938; Collias, 1944). Noble (1939), working with fish, reported that the more dominant individuals in a group of *Xiphophorus* lose less weight during periods of starvation than do more subordinate individuals. Noble also found that the larger and heavier fishes tend to occupy the positions of greater dominance. Evidence in the present paper indicates that a similar situation exists for *Platypoecilus*.

Both individual and group selection are important, since, if a species is to survive, it must have both quality and numbers. Within a social unit, selection of individuals will act to maintain quality, while selection of entire groups will maintain sufficient numbers.

SUMMARY

1. Small homosexual or heterosexual groups of *Platypoecilus* fishes exhibit nip-right behavior.

2. The fishes form hierarchies based upon individual contact-pair relationships which are established by challenging and fighting.

3. The hierarchies show a tendency toward the true straight-line type, but incomplete hierarchies and triangle situations are common.

4. After initial hierarchies are estab-

lished, the social behavior of the fishes is less savage than during the formative period.

5. Under the conditions of these observations all contact relationships tended to be short-lived and were characterized by frequent reversals, due to revolts.

6. Established societies are characterized by alternating periods of activity and inactivity.

7. Despots of either sex will interfere with the contact reactions of their subordinates.

8. A despot of either sex nips its subordinates differentially as individuals and not according to their several ranks.

9. Males are less social than females. They nip less but more savagely, move about less, and their hierarchies are less stable.

10. In heterosexual groups males and females nip individuals of both sexes except during breeding periods, when males tend to limit their nipping to other males.

11. In heterosexual groups the differences between male and female behavior are similar to those in homosexual groups but are less marked.

12. Males tend to occupy the higher ranks in heterosexual hierarchies.

13. The amount of nipping done by a fish corresponds to its rank.

14. A strange fish reacts submissively to all members of an established society. They, in turn, react aggressively toward the stranger.

15. No evidence of territorial behavior was noted.

16. Some evidence exists that the fishes recognize each other as individuals.

17. Factors involved in dominance are: general aggressiveness and other psychological factors, size, maleness, and factors as yet unknown.

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